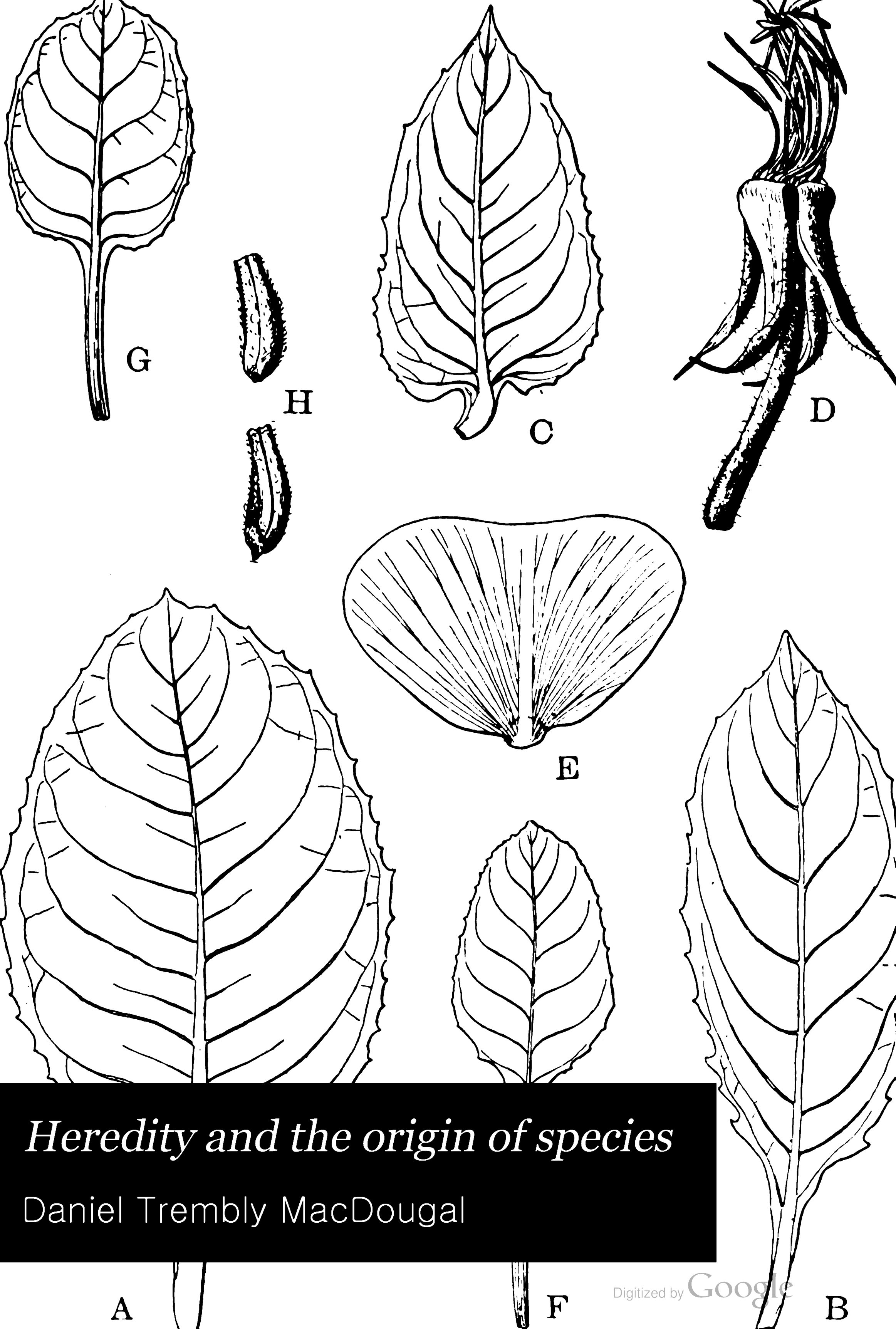

Heredity and the origin of species

Daniel Trembly MacDougal

HEREDITY

AND

THE ORIGIN OF SPECIES

LECTURE GIVEN BEFORE THE BARNARD
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BY

DANIEL TREMBLY MACDOUGAL
DIRECTOR DEPARTMENT OF BOTANICAL RESEARCH,
CARNEGIE INSTITUTION OF WASHINGTON

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HEREDITY, AND THE ORIGIN OF SPECIES.*

THE surface of the earth is inhabited to-day by hundreds of thousands of forms of life, which upon analysis are found to be separable into groups or species, with well-marked and characteristic attributes, which may be transmitted from generation to generation. The strata beneath the surface are found to contain the remains of thousands of other forms, now extinct, but which show certain general relationships to the existing organisms. If we piece together the actual records, and take the backward bearing of our information, we arrive at a period sometime within the last six hundred thousand centuries, when living matter was more indeterminate in the forms which it assumed, and was, perhaps, quite unlike any protoplasm we meet at the present time.

From this primitive substance series of organisms have been produced, which, in the successive stages of the earth's history show an increasing complexity as the present epoch is approached, and which embrace more numerous forms with the advance of time.

In this upward movement, this evolution from the simple to the complex, in the production of many from few, it is not to be taken for granted that protoplasm has been a perfect automaton, and that it has nothing but successes scored to its credit in the ever-changing conditions it has

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met since its beginning. On the contrary the succession of its forms is a most devious one, and by no means easily traced. Phylogenetic systems are made up chiefly of allowable suppositions, and it is altogether probable that we do not know more than a fraction of the course of the zigzag, halting, and at times, receding steps followed by living matter in its development into existing types.

Thus the mosses are seen to have reached the ultimate development allowable by their morphological character, and hence are incapable of any movement which will produce higher or better organized types. Accordingly we may assume that their existence as a constituent of the flora seems to be doomed to a diminishing importance, if not final extinction. The fern-like plants are also examples of a great phylum of the vegetable kingdom which, in the Carboniferous period, being most suitable for the conditions present, constituted the prevailing type of vegetation, making up perhaps as much as three-fourths of the plant-covering of the land. Their organization is one which promises nothing of advantage vegetatively and reproductively, and we are now at a time when we see them slowly but inexorably, being supplanted by seed-producing forms.

With the advance and retreat of the ice-sheets, the upheaval and submersion of land areas, and other great alterations in the earth's surface the hosts of plants have marched and countermarched across the face of the world, now losing thousands of species, the remains of which we exhume from ancient battlefields; now entering upon new possessions and increasing the numbers of species and forms by originating new types, which survived or perished according to their fitness or unfitness. In the interpretation of the traces of these major movements of living forms great care must be exercised in distinguishing the essentially different factors affecting the distribution of

plants and animals. It is as if two games of checkers were being played on an enlarged board at the same time, the moves of each player being governed by those of his opponent and interfered with by those of his neighbor, and the two players on one side of the board by no means advance, guard and retreat in parallel fashion, while their losses and gains may be wholly disproportionate. With regard to the application of this warning note it is to be said that the "naturalists," as some zoologists term themselves, having made the greatest number of essays to offer a universal interpretation of the problems of distribution are to be credited with the greatest number of defenceless assumptions. In all developmental and evolutionary researches too much emphasis can not be laid upon the basal fact that the physiological and morphological nature of the two great classes of living things are so widely divergent, that the derivation of universal biological principles from their apparently concurrent behavior, must be made with the greatest caution.

Let us pass at once to the basic problems of life, those of the origin of characters and their inheritance, by which new species arise. Very naturally the first statement advanced was a purely theological one, that species were created directly, and that we need not expect to find an explanation in natural causes.

Of the hypotheses that may be taken more seriously, one that has even lately been regarded with much favor, predicates that organisms undergo transformations, or alterations by adaptive changes in their organs and entailed functions, as a direct reaction to environmental factors, and the altered features becoming fixed and inheritable, the organism receives a lasting imprint from its habitat. Migration to new areas, or changed climatic conditions might give opportunity for new stimuli and different reactions which might, or might not, affect those pre-

viously made. We need not, at this time go into the intricacies of the arguments that cluster about this main thesis, or weigh the evidence that is drawn from the presence of useless, vestigial, and useful characters in various organisms.

Popular belief in the influence of environment and the inheritance of acquired characters finds its commonest expression in "that plants have been changed by cultivation." Domesticated races are spoken of as "garden forms" by botanists and horticulturists, with the implication that they are specialized types resulting from the effects of tillage. Now so far as actual cultivation is concerned, this assumption is without foundation, since at the present time no evidence exists to show that the farm, garden or nursery has ever produced alterations which were strictly and continuously inheritable, or were present, except under environic conditions similar to those by which the alterations were produced, although vague statements and erroneous generalizations to the contrary are current. It is true of course that structural and physiological changes may be induced in a strain of plants in any generation, which may persist in a share to the second, or even in some degree to a third, but no longer. Some very important operations of the market gardener and the farmer are dependent upon this fact.

The possibility that permanent changes might be induced is by no means to be denied, and it is a fair subject for investigation. Actual evidence is to be obtained only by observations of breadth under guarded conditions. Until this is at hand all affirmative conclusions can be but inferential and suggestive.

Vicinism, the somatic multiplication of bud-sports and extreme variants from a fluctuating series, and the confusion of closely related elementary species form the basis for the greater number of mistaken assertions as to

the effects of cultivation. It is obviously necessary to examine all facts bearing upon the lineage of supposedly new forms, with the greatest care before their aspect, or behavior may be taken as evidence upon phylogenetic problems.

The theory of natural selection of an intra-specific application, as one of which new forms might arise, is so well known that we need not particularize in defining its ramifications. Briefly, it is assumed that as the whole mass of individuals comprised in a species is in a constant state of variation the individuals which show features even the most slightly better adapted to the environment, survive while the less fit perish. Thus by infinitely small changes during each generation a species moves away from the ancestral type in one or more directions until in the course of thousands of years the differences become so great as to be appreciable, and of a specific character, to use an arbitrary phrase. Three unsurmountable objections to the acceptance of this method as universal present themselves. First, the fluctuations exhibited by the individuals comprised in a species do not in any known instance transgress definite measurable limits, and do not depart from an ascertainable norm or average. Secondly, the gradual transition of individuals from one type to another, that is intergrading forms, demanded by this theory, are not found among plants, and thirdly, although we have preserved specimens and records of several species which cover their history for many thousands of years, yet such gradual transformations are not observable. Lastly it is to be said that it is extremely doubtful if the earth is old enough to have permitted the development of the great number of organisms which inhabit it, by this method.

A secondary idea that has been formulated in connection with this subject is that of orthogenesis, by which the organism evolves rudimentary structures purely as a result of internal forces, and initially without reference to util-

ity, or to environment. These rudimentary organs may, in the course of generations wax in size, undergo increasing differentiation of structure, perhaps finally becoming sub-functional or even fully functional, although nascent organs are not always supposed to attain this useful end. In support of this theory it has been pointed out that plants and animals show many structures, which so far as our understanding of them goes, are wholly without part in the life of the organism. The present development of plant morphology, however, is one which is carrying us farther and farther away from the conception of such pre-functional formation of organs, as the whole tendency of modern investigation is to place the morphogenic processes upon a physiological basis. On the other hand the argument that the variations of the organisms are "determinate," and are governed by the morphological possibilities is one which surely holds for any method of phylogenetic procedure. Thus it needs but the briefest common-sense consideration to show that any given type of leaf or flower, could not possibly vary toward all other types, but only in the direction of certain forms not too widely different.

A more explicit statement may prevent a misconception. It has been held by some writers that variations and mutations, theoretically follow those already made, as a projection of them, or a continuation, which carries the organs concerned, successively and ever nearer some ideal form or type. This is determinate variation in its strictest sense. On the other hand, it is argued that from any given stage in its development an organ may vary or mutate in any direction limited of course by its morphological possibilities, and such alteration may lead the structures concerned in any given course from that previously pursued. It need only be said that to the experimenter the latter view seems to be the more fully justifiable by the facts observed in mutations.

Of the many other phases of the existence, and distribution of organisms, that have been considered in a controversial way to prove this, or that, hypothesis it must be ceded that in this discussion of the effect of isolation upon the origin and preservation of forms, the evidence adduced, so far as plants are concerned does not especially favor any of the suppositions discussed previously. In like manner the bogie of the effects of close- and cross-breeding is used in the most reckless manner to support the most diverse generalizations. Until investigated with the exactness demanded by modern technique, and by the most approved methods with material of undoubted pedigree, we may well consider close- and cross-fertilization as operations the value of which is yet to be estimated. Nearly all of the available data have been obtained with domesticated races, artificially selected from what, in the natural conditions, may be the most extreme phase of a character, and far from the norm of the species in many particulars. The retrogression toward this norm may be a deterioration of the economic value of the strain, yet from the point of view of the species itself it may be a direct movement toward the average condition, in which we may not secure so much speed, beef, wool, milk, grain, or fibre, as in strains bred and selected for these features.

It is with great relief that we turn from these historical and hypothetical considerations to the authenticated facts, the interpretation of which affords some positive generalizations as to phylogenetic procedure. In other words we take up the observations by which species *have* arisen, in place of the suppositions as to how they *may have* arisen.

First, it has been known for over half a century that fixed forms, constant in inheritance and self-maintenant, therefore constituting species have resulted from hybridization. The fertilization of the egg-cell of one species by the pollen of another, often results in an interlocked and

stable combination of the characters of the parental forms in such manner as to give rise to a new type unlike either of the parents, variously intermediate and constant to the new type in succeeding generations. More than a thousand such fixed hybrids, or hybrid species are known, some of which have been formed anew experimentally and are thus beyond doubt. It is to be seen therefore that hybridization has played, and is playing, no small part in the composition of the flora of the earth, and that it must be considered as an active, and not unimportant factor in the evolution of plants.

It must be admitted at once that such fixed hybrids are exceptions to accepted principles of dominance, and of the purity of the germ-cells, as the fixed hybrids depart entirely from the Mendelian procedure. As a further complication we have in some instances a hybrid progeny comprising several fixed types, each constant to itself. The only possible explanation of such phenomena in the simpler case calls for a fusion of the germ-cells and a double longitudinal division of chromosomes.

Such splittings are qualitatively unsymmetrical, since the fixed hybrids are variously intermediate between the parents, sometimes being goneoclinic to the one furnishing the pollen, and in other cases to the one bearing the egg-cell. When it comes to the composition of a hybrid progeny which comprises several fixed types in the first generation, breeding true in succeeding generations, we can only look to the researches of Wilson and others upon the quantitative and qualitative inequality of the chromosomes to furnish us the proper clue. It is only fair to say that no investigation of such cases has yet been made. Now as to a third category in which the hybrid is polytypic in the first generation, and some or all of the types may split in the second generation into forms, which may or not be identical with the grandparents, we evidently have a com-

plex case in which the partial fusion of unequal chromosomes, with divisions of the chromosomes may operate in a manner to secure anything but purity of the germ-cells. The results of such complicated integrations and splittings are incidental to the scope of this lecture however, as we are concerned at present only in those cases in which fixed forms result from hybridization, chiefly in the first generation. So far have we advanced, however, in the study of the behavior of hybrids, that with the information obtained from them, and with the recent discoveries as to the differences of chromosomes, we may well believe that we are now at the dawn of a new day in the study of heredity and all of its associated problems, in which the greater results are to come from the proper and closer correlation of the researches of workers in all branches of natural science.

The second method by which new characters and new species have been seen to arise in the succession of generations in plants is that of discontinuous variation, or mutation. In following out the germination of hundreds of seeds in pedigreed strains of plants, a few individuals may be found in each generation, which are notably different from the type in anatomical and physiological features. These divergencies are variously heritable, constituting breaks in descent, by which, in some cases, new species originate. Such seed-sports or seed-mutants have been seen hundreds, perhaps thousands of times during the last two centuries, but it is only within the last twenty years, that their phylogenetic importance began to be appreciated. It will be of interest to this assembly to know that American botanists and horticulturists have made early observations of direct interest in this connection. Thus Dr. Arthur Hollick, while a student at Columbia University in 1879, said in writing of white varieties of colored plants: "First then, we have to consider those sports of nature where

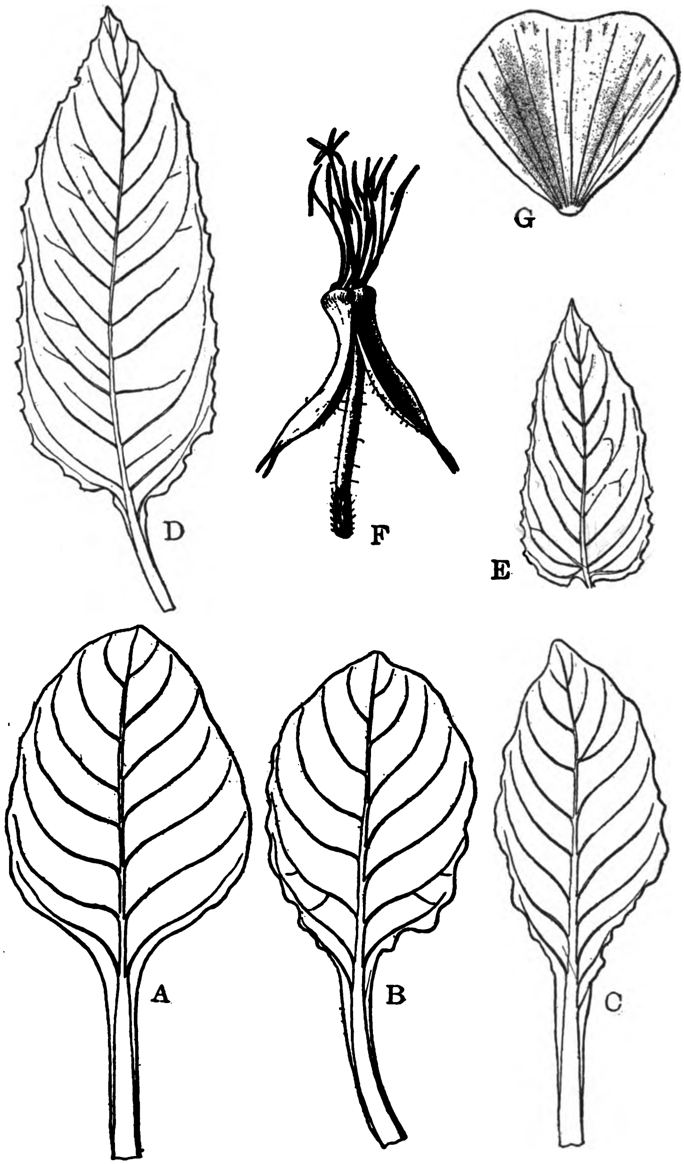
there has been a sudden change, without any intermediate steps, from a plant with colored flowers to a pure white variety: such may be termed "negative" varieties, since their peculiarity is due rather to an absence of color, than to the presence of white. Not only does the flower show the characteristic absence of color, but the leaves, stem, and, in fact, the entire plant, are invariably of a lighter green; and if any red be normal to the stem (which is often the case), this will also be of a lighter shade. It has often been urged that these albinos are mere 'sports' of nature with nothing constant about them,...., and that there is nothing inherent in the constitution of the plant. Fortunately I have been able to test this,..and found them, ..not only constant in their peculiarities, but also that these are bred in the plant and capable of inheritance." Three years later, about the time that De Vries began casting about to find material suitable for the demonstration of his theory of unit-characters and their saltatory action, Mr. Thomas Meehan, a horticulturist of Philadelphia, wrote as follows, in a discussion of some anomalous form of the oak: "The conclusion that I have been forced to is that the odd forms we often find in nature are not necessarily hybrids, but are as likely, if not more likely to be the outgrowth of some internal law of form with which we are as yet unacquainted. That they do not often perpetuate themselves is (*not*, plainly implied) remarkable when we remember that of thousands of seeds produced on any one tree, but a very small percentage ever gets a chance to form, and of those which do sprout, again but a small percentage survives to become bearing trees. As the number of trees reproducing the general features of the original may be as a hundred to one of the more strikingly aberrant forms, we may see that though individual instances may be common, we are never likely to meet many trees of one stamp. Once in a while an indi-

vidual tree may find itself in a situation favorable to the preservation of a number of seedlings, which might endure until again reproductive; in such cases a marked variety may originate and make its way over the earth.

"I have often thought it probable that in time a few individuals of these suddenly introduced forms might again leap into new features, and then if they should be able to sustain themselves, we should have new species quite independently of any principle of natural selection; that principle, as I understand it, being governed chiefly by 'environment.'"

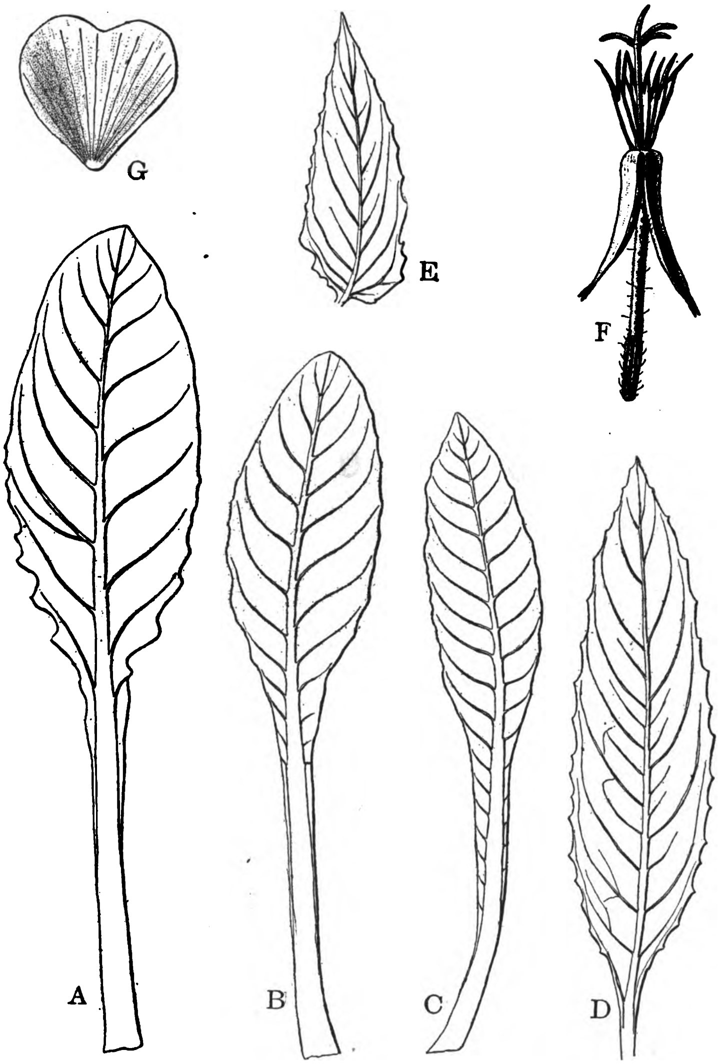
These utterances may be taken as prophetic in part, and in part as a natural expression of the inadequacy of explanations of the origin of species current at the time. Shortly afterward, Professor De Vries, impressed with the necessity for obtaining positive evidence upon the subject, began an examination of the plants in the vicinity of Amsterdam, Holland. Over a hundred species were brought into cultivation, and tested by guarded pedigree-cultures, and every precaution was taken to exclude interference of agencies which might introduce errors. It is impossible to describe the enormous amount of work entailed in such investigations, but the truly splendid results well justify the tedious care by which lines of descent were carried through successive generations for two decades without allowing a trace of doubt as to the purity of the lineage involved.

During the last four years a partial duplication and an extension of these experiments has been carried on in New York. It seems unnecessary at this late date to go into the detail of the mutations of Lamarck's evening-primrose, especially since the phenomena exhibited by them are also to be seen in many other species. By way of illustration it need only be said that this plant, as originally observed by De Vries, was found to give from two



Oenothera Lamarckiana, the parental form which is giving off many mutants. A, B, and C, leaves from rosette. D, leaf from middle of flowering stem. E, bract. F, flower with petals removed. G, petal.

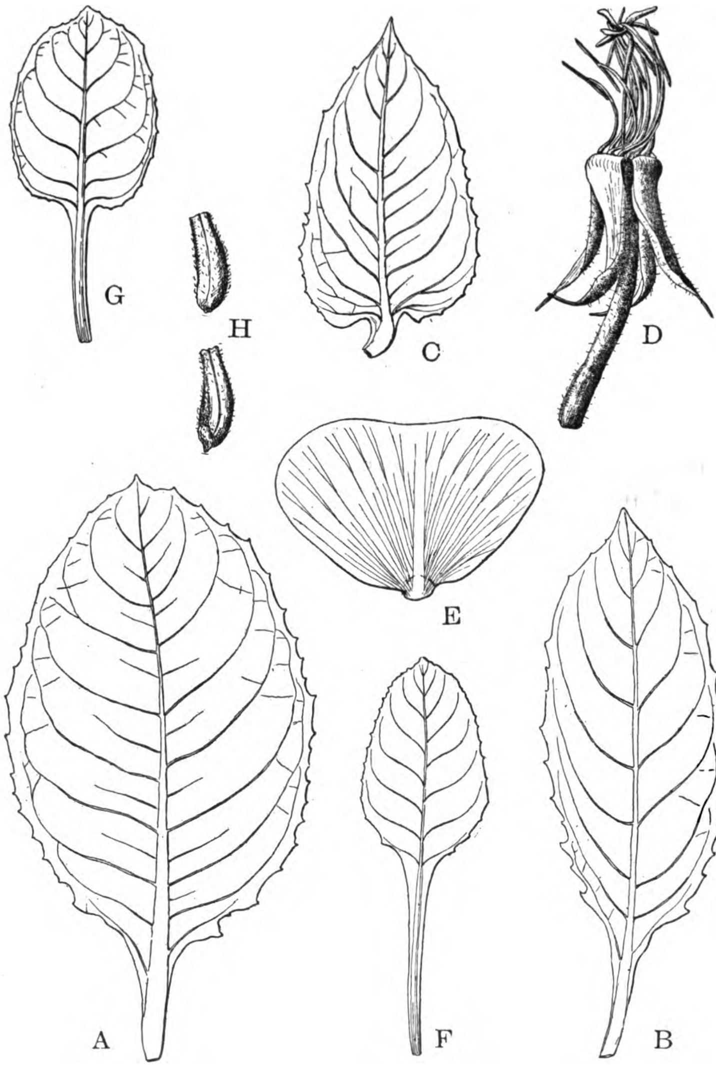
to five plantlets in every hundred which were widely divergent from the type, and could, upon maturity, be ar-



Oenothera rubrinervis, One of the Mutants of *O. Lamarckiana.* A, B, and C, leaves from rosette. D, leaf from middle of flowering stem. F, flower with petals removed. G, petal.

ranged in several groups, and in fact constituted several possible species. One, *scintillans,* was eversporting, and

continuously and consistently gave rise to a variety of forms in its progeny, which included the parent and its

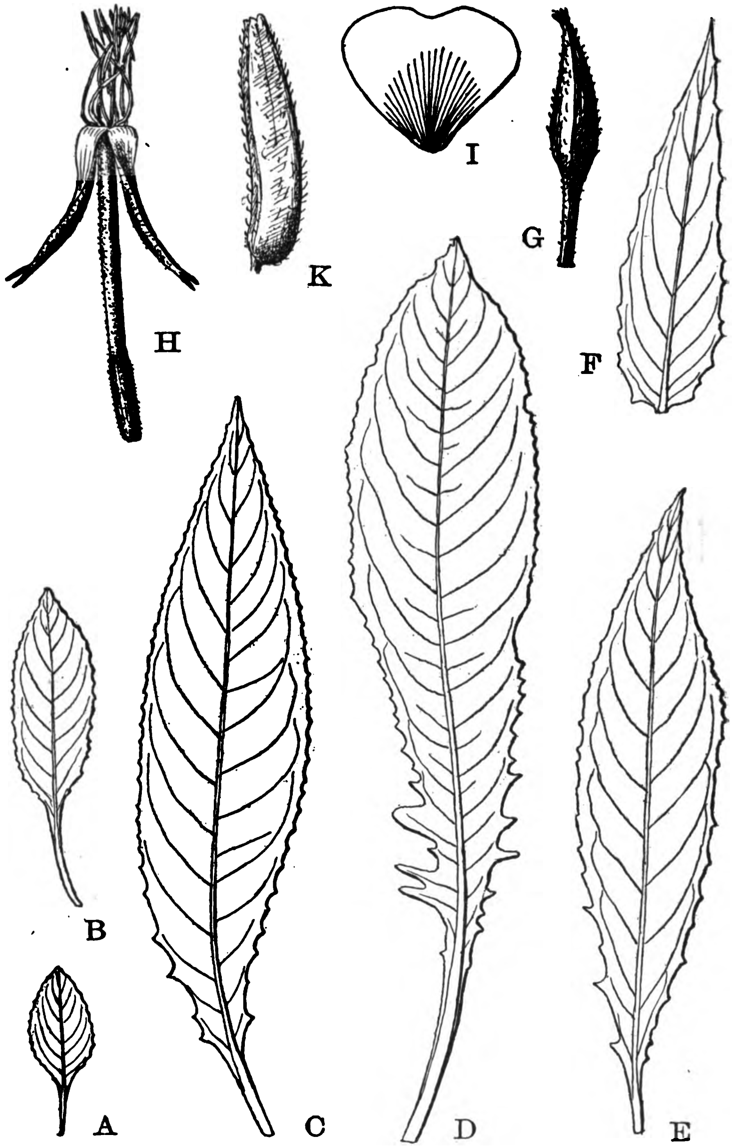


Oenothera gigas, One of the Mutants of *O. Lamarckiana.* A and B, leaves from middle of main stem. C, bract. D, flower with petals removed. E, petal. F and G, leaves from the rosette. H, capsules.

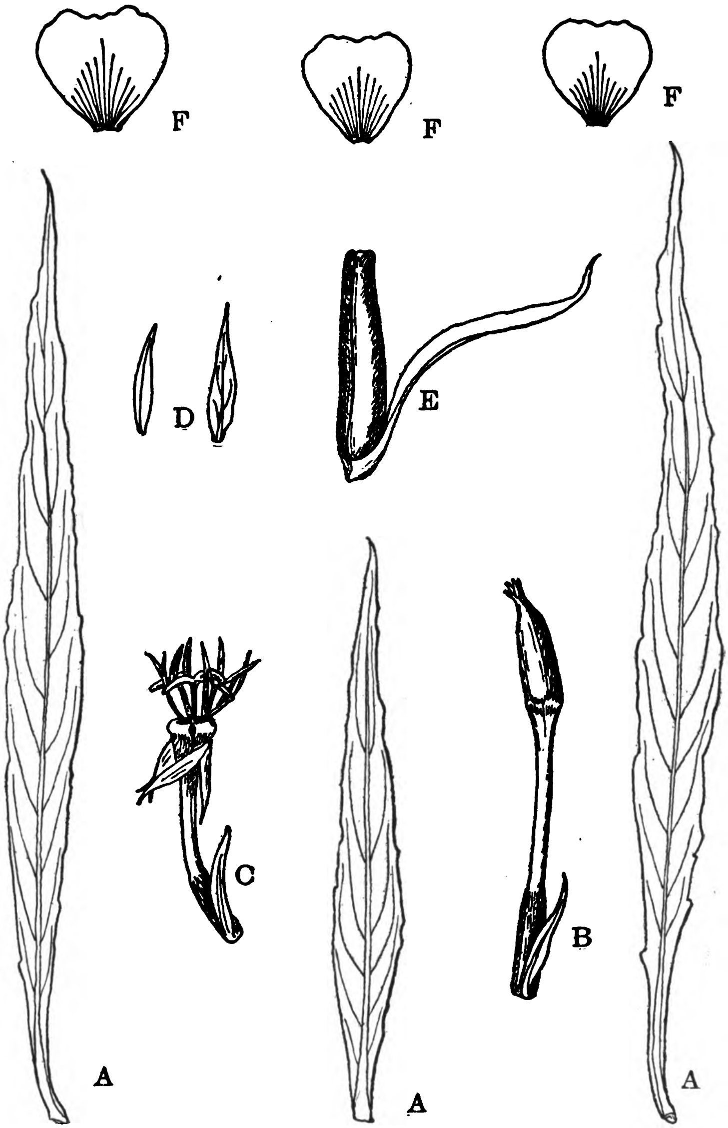
mutants. Another, *lata,* was imperfect and did not mature pollen, and hence was incapable of independent existence.

Others were perfect and vigorous both vegetatively and reproductively, and have been found capable of sustaining competition with the parental type. Of these *rubrinervis* grows more rapidly, germinates its seeds more quickly, and makes more numerous branches, and bids fair to be able to win out in a struggle with the parent in all of the phases of the struggle. *Gigas* is a more vigorous form than the parent, and both it and *rubrinervis* show a tendency to predominate when crossed with the parent. *Brevistylis* was found in the original location from which the mutating strain was taken, and as it has not appeared in any of the pedigreed cultures of the parent type in twenty years and still maintains itself in the original locality, it may be designated as a mutant which not only has arrived, but has survived under perfectly natural conditions. Recent cultures in the New York Botanical Garden from seeds of Lamarck's evening-primrose, sent from various parts of the world where the species is under cultivation, demonstrate that it is not alone the plants observed by De Vries at Hilversum are mutating, but the same derivatives are being given off in widely separated localities.

Purely-pedigreed strains of other species of evening-primroses have also been tested with the result that I am able to announce that three species are mutating, in lines of descent which came from wild plants one and two years ago. The common evening-primrose, *Oenothera biennis*, gives rise to one atypical individual in every two hundred seedlings, which during its entire development is continuously different from the parent in many features. It reproduces itself, after the manner of *scintillans,* appearing to be eversporting and giving many of the parental individuals in the purely fertilized seeds. Within the last two months a single rosette representing a new and unknown type has appeared in the seed-pans appearing to be a mutant which is found not more than once in twelve or fifteen



The Common Evening-primrose (*Oenothera biennis*), which is giving off one or more mutants. A, B, C, and D, leaves of the rosette. E, leaf from middle of flowering stem. F, bract. G, bud. H, flower with petals removed. I, petal. K, capsule.



A Mutant of the Common Evening-primrose. A, A, leaves of the rosette, and from the stem. B, flower-bud. C, flower with petals removed. D, bracts. E, capsule with bract in profile. F, petals.

thousand plants. The evening-primrose of the Adirondacks and northern New England, *Oenothera cruciata,* has been found to give atypic individuals conforming to a single type, which is also represented by specimens that have been collected in a wild state, so that here also, we have the survival of a species which is still arriving in a large proportion of the progeny. The great-flowered evening-primrose, *Oenothera grandiflora* of the southern states has been grown during two generations and it also is found to give derivatives, one or more of which appear to be already represented in the flora of the region.

One of the most interesting correlations to be made from a study of the results of these observations is to be found in the parallel mutations exhibited by the several species, in apparent contradiction of the principle of radiate variation and mutation (*allseitige Mutationen*). Among these are to be mentioned the origination of a form with cruciate flowers of the same general form as the *Oenothera cruciata* of the Adirondacks, from the species known as *O. biennis* in Holland, which is not identical with any species known to grow wild in America. The same species has also been seen to give off a mutant having the character corresponding to the mutant *nanella,* coming from *Lamarckiana,* according to De Vries. Then an evening-primrose of unknown identity has been found on Long Island by Dr. Shull, far removed from the locality inhabited by any other cruciate plant, and strongly suggestive of a mutation from *biennis* or some other form native to that locality. Such facts merely show that the forms borne by nearly related species lie well within the limits of the morphological possibilities in saltations and that they may be expected to be duplicated in other observations.

Scattered through the literature of botany and horticulture of the last century are scores of records of the

sudden appearance of sports and forms of the aspect of species which fully support all of the conclusions drawn from the observations on the evening-primroses. An examination of the facts easily brought together allows us to see that certain general principles in the organization of the plant, and in its behavior in these breaks or saltations in heredity may be made out.

The first and most important of these is one which was advanced by De Vries speculatively, before he began his experiments in heredity, namely that the plant is essentially a complex group of indivisible unit-characters. These unit-characters may not always be expressed, or recognizable in external anatomical characters, since they may be in a latent condition, or totally inactive, or external taxonomic characters may really consist of several elementary qualities, but these are not shown in any intermediate stage although they may be modified within the limits of fluctuating variability.

Any plant, supposedly, includes thousands of unit-characters, and as they are essentially qualities, or capacities, they do not usually coincide with the characters ordinarily used in taxonomic descriptions. As an illustration, the phases of geotropic sensibility of an organ may be considered as a unit-character. Thus a branch is either apogeotropic, directing its tip directly upward, or it may be diageotropic placing its axis in a horizontal plane, at right angles to the action of gravitation, or it may undergo a mutation and "weep" or direct its tips directly downward. In any case, however, it possesses one of these three forms of reaction. It does not follow, however, that all branches are actually in one of these three positions, for other forces to which it reacts may operate to place the axes in various planes, and the position of the branch may express just such concurrence of elementary characters as alluded to above, or indeed the geotropic unit-character may be latent,

and the organ may respond to other forces exclusively. Similar analyses must be used in the delineation of all unit-characters, and it is obvious, without further discussion, that we will never be able to uncover, either theoretically or actually, more than a few of these indivisible units. The forms and activities by which we recognize plants must by no means be taken to be simple in their constitution unless proved to be so, and the modification of a character in hybridization and otherwise must be taken as proof that it is not an elementary feature.

In tracing the development of species it is found practicable to designate them as retrogressive when a distinct unit-capacity, or unit-character is lost or, rather, becomes latent. Thus the loss of color must be of this kind, and also the loss of geotropic reaction, while the power of forming laciniate leaves when shown by mutants from a simple-leaved type would be estimated as a progressive mutation, as the group of characters concerned belong to a more highly organized type of organ. If a white-flowered species should give rise to a form with colored flowers it might well be taken as a degressive movement, or as a retracing of a step once lost, since all flowers were in all probability originally colored. Here again the actual test is hybridization, it being accepted that the retrogressive forms of organs are recessive or latent when crossed with the parental or nearly related types.

As to latency we can only say that strains of plants do carry capacities of one kind and another for many generations without these particular forms of unit-characters showing any activity. Thus a mutant which springs from a parental type, and shows a laciniate leaf instead of the ancestral leaf, must carry the latter form in a latent condition. The latent character may be awakened from time to time, or may be entirely and permanently inactive. The most easily analyzable examples of latency are seen in

hybrids. Thus when the blue-flowered *Veronica longifolia* was crossed with a white-flowered variety derived from it, the progeny was entirely and continuously blue-flowered except for occasional bud-sports. The white-flowered condition was here very evidently in a latent condition. In other instances white-flowered forms have appeared as a recessive, forming one-fourth of the progeny. If qualities have a cytological basis, and we may certainly assume that they do, then it is not easy to speculate intelligently on the probable condition of latent characters.

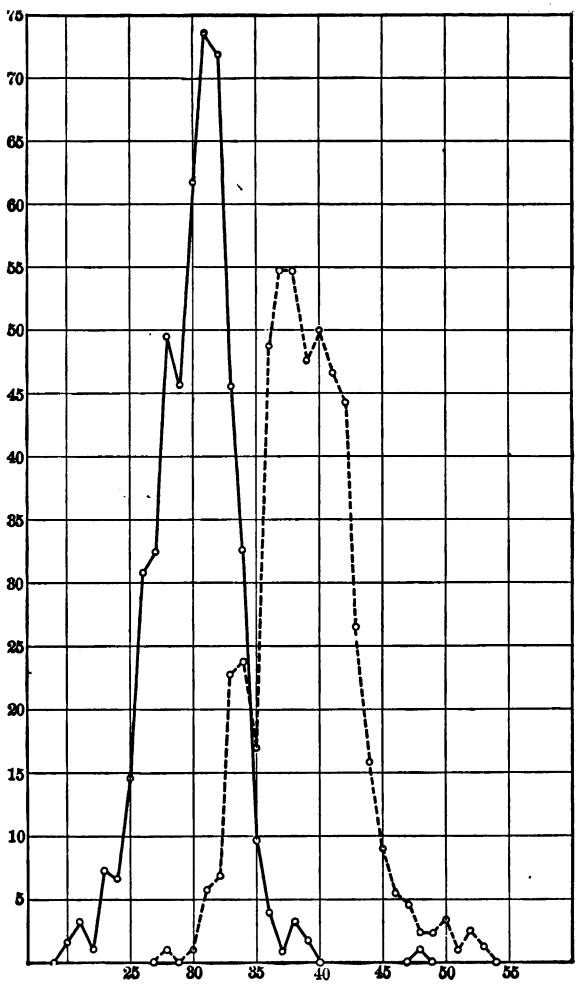
A very striking feature of mutants consists in the fact that the gross anatomical characters in which they diverge from the parent shows a much wider range of variability around its new norm, than does the homologous character in the parental type. Many observations bearing this interpretation have been on record for some time. Chas. Darwin in his *Origin of Species* noted that varieties varied more widely than the closely related species from which they were supposed to be derived, and many other observers have touched in one way or another upon the subject. Dr. Shull's recent researches upon this subject led him into the making of exact measurements, by which he also finds that the wide fluctuations of the mutant characters are accompanied by a lesser degree of correlation than prevails in the parental forms. Thus, for instance, the leaves of *rubrinervis* not only vary relatively more in width than those of the parental *Lamarckiana*, but the proportion between the width and length is not so constant as in the latter. Other organs of these and other species were subjected to exact measurements with similar results, while a large number of recent observations are known which justify the conclusions just stated. Of these the great variation of the length of the pistil in *brevistylis* in comparison, and the wide fluctuations in laciniate leaves are good examples. Many of the latter are known to be direct deriva-

tives of simple leaved ancestors, and are therefore capable of easy observation. With these facts in hand the possibility suggests itself that we might be able to distinguish between a structure recently arisen and one which was borne by a related species for thousands of years, but the exactness of such estimates is a matter of conjecture.

It seems to be taken for granted by a great number of workers interested in this subject, that species showing wide variations of the organs are the ones most likely to offer a high frequency of mutations, and my correspondents in various parts of the country are constantly calling attention to these forms under such a mistaken impression. As a matter of fact we may confidently expect that the species which show the greatest variation, or are eversporting, are the youngest.

Now having obtained the result just described we find ourselves face to face with one of the most interesting and difficult questions in heredity. If the newly arisen mutant forms are more widely variable than the older ones, how do they ultimately become narrowed? If the greater number of species originated by mutation, as we confidently believe they did, then they must have shown a much wider range of variability than they do at present; by the operation of what agency has variability been decreased, and correlations made more strict? At the present time I am compelled to say that I can not make an intelligent suggestion. Again if new characters vary widely at first, and lose this power, would it be possible to estimate the age of any given character of a species from the degree of variability? The author of the investigations just noted suggests that the best prospect for evidence of value upon this point might be obtained by a comparative statistical study of more recent types of structures in the foliar or reproductive organs, and of older forms that have come down from

the previous epoch. It certainly offers a most alluring field for research, and will doubtless soon receive attention.



Range of Variation of the Ratio of Width to Length of Leaves in the Parental *Lamarckiana* and One of Its Mutants. The dotted line shows that the range in the parent is 28-53, with a coefficient of variability of 9.53 ± 0.22 per cent., while in the mutant represented by the solid line, the range is 20-48, with a coefficient of variability of 10.30 ± 0.22 per cent.

Let us return to the question of the diversity of mutations which may ensue in any species. Theoretically a

plant might show discontinuous variation in almost any direction, but this departure of course does not exceed an amplitude determined by the morphological possibilities. With all of these features taken into consideration however, it is to be seen that it might be possible for any plant in a mutable condition to give rise to dozens, or perhaps

		X_2	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	9	
			50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	
			55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	
X_1																						
−12	17					1																1
−11	18			1																		1
−10	19																					0
−9	20			1		1	3	1														6
−8	21		1					1			1											3
−7	22				1	2																3
−6	23						2	2	7	2		1										14
−5	24						1	2	6	2	1	2			1							15
−4	25						3	2	6	6	3	5	2			1						28
−3	26							3	5	6	11	3		1	2	1	1	1				34
−2	27							2	15	11	7	9	6	3	3				1			57
−1	28							3	4	10	8	16	5	9	1	2						58
0	29							1	2	11	19	10	3	6	5	1						58
1	30								1	13	12	10	16	10	8	1	2		1		1	75
2	31				1					2	11	18	21	6	3	1	1	1	1			66
3	32									1	8	17	20	8	7	3	3	1				68
4	33										1	9	9	7	6	3	2					37
5	34											1	6	15	5	7	1	2				37
6	35										2	3	4	13	5	2	1					30
7	36											1		1	3							5
8	37										1	1		1	2	1	2					8
9	38														2		1	2				5
10	39														2	1	1					4
11	40																1					1
			1	2	2	4	9	17	46	64	85	166	92	80	55	24	16	7	3	0	1	614

Correllation Table of Length and Width of Leaf in *O. rubrinervis.* $p = 0.6604 \pm 0.0119.$

scores of types simultaneously, while on the other hand it may originate but one aberrant form at a time. Lamarck's evening-primrose is producing a dozen, and the common species but one or possibly two, while the great-flowered species is throwing off three or four, as far as

our observations go. It will be profitable to analyze the consequences of the origination of diverse types simultaneously. In the case of *Oenothera grandiflora* it ranges from Kentucky southward to the Gulf over climatic and edaphic conditions of wide diversity. If it be assumed

		X_2	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	9		
			45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135		
			50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140		
X_1	.																						
−13	24		1					1															2
−12	25				1																		1
−11	26			1	1																		2
−10	27					1	1		1														3
−9	28					1	1		1		1												4
−8	29						1	2	3	2	1												9
−7	30						1	2	2	2	3												10
−6	31							1			2	2											5
−5	32								2	2	4		2										10
−4	33						1	1	6	3	4	4	3										22
−3	34							1	1	5	8	3	3	1									22
−2	35							1	2	4	9	6	1	4	3	1		1					32
−1	36						1	1	1	2	5	10	4	5	1		1						31
0	37							1		3	11	9	11	8	5	3	1						52
1	38							1		4	3	11	10	16	3	1							49
2	39										3	7	7	8	4	1	1						31
3	40										6	4	9	6	12	3	4						44
4	41											1	8	10	5	5	1	4	1				35
5	42											2	7	9	5	3	2	1			1		30
6	43									1			1	8	4	2	2				1		19
7	44													3		6		2		1			12
8	45													1	1	1	1	2					6
9	46															1							1
10	47																				1		1
11	48																2				1		3
12	49													1					1				2
13	50												1										1
			1	1	2	2	6	12	19	28	60	59	67	80	43	27	15	10	2	1	4		439

Correllation Table of Length and Width of Leaf in *O. Lamarckiana*. $p = 0.7916 \pm 0.0090$.

that all of the mutants are being given off by the whole species then these must be thrown into the struggle for existence under conditions widely different. In some cases one mutant finds itself equipped to survive in the given

environment, and it does so in competition with the native flora, including the parental form. In a different part of the natural range of the parental form, a second mutant might have the advantage, and it alone of the entire brood would survive, while a third would be the best form for still another set of conditions. So well in accord with the facts do we find this assertion, that it is not hazardous to predict that when a final survey of the distribution of *Oenothera grandiflora* and its mutants is made, some such arrangement will be found. With this idea we must also concede that many of the mutants, so far as our experience goes, do not meet at all the conditions suitable for their existence, and these perish. In brief we have natural selection, not a selection *within* species, but a selection *among* species, by which certain ones are elected for survival and others doomed to destruction no matter how numerously, or how long they may be thrown off by the parental type.

As to the periodicity of mutations our information is not very extensive. Does a species, as it produces generation after generation in the course of centuries, arrive at a point where it begins to give off atypic individuals, and is this process continued for a time and then discontinued? We can only say that we find some species mutating and others not, we have not seen either the opening or closing of the mutative period in any species. This consideration is complicated however with that of the frequency of the mutants. Thus in Lamarck's evening-primrose five in every hundred plants are mutants, one in every two hundred of *biennis,* and it is conceivable that the atypic form might not occur more than once in a thousand, or once in ten thousand, or once in a million. These large numbers of plants of any species are not all in existence at any one time, and it might take years, or even decades to bring one mutant within the range of the possible number, in which case a false conception of the mutative period might be

gained. It is suggested therefore that the conception of *frequency of mutation* is the primary idea, although the action might become intensified in certain periods, of more or less definite limits.

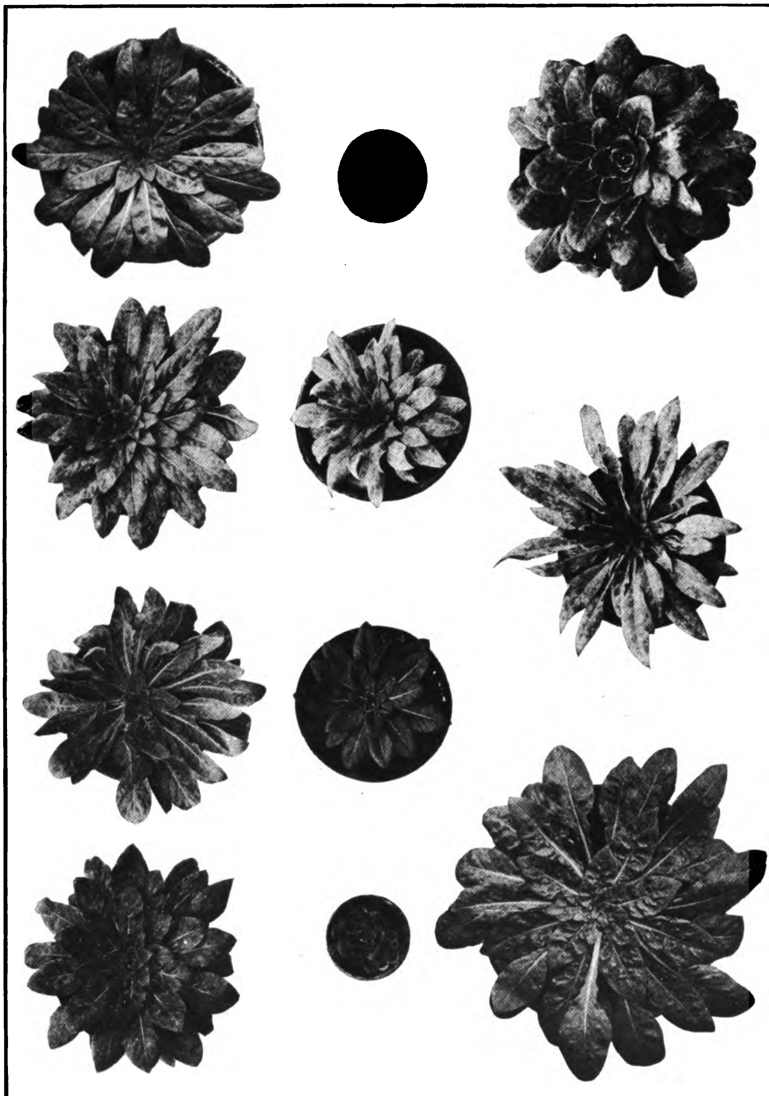
Finally we may consider the causes inducing or affecting mutations. Mutants are found to be the most numerous under conditions most favorable to the growth and reproduction of the parental type, and this is also true of all anomalous structures. It is thus to be seen that mutations probably do not give rise to species most readily under the stress of unfavorable environment, or under any conditions which weaken the parental form, but when it is at a maximum of activity.

In the attempts to localize the changes in the cells, or in the chromosomes, which result in the formation of atypic individuals from seeds we are confident for theoretical reasons that these ensue previous to the reducing or qualitative divisions in the formation of the egg, or in the pollen mother-cells. Just what this change may be, we are unable to say, and shall probably know no more about it until the cytologist shall have given us some clue to the manner in which the separate qualities are represented in the chromosomes, in which the mutative changes must ensue. It is self-evident that in a mutation, some characters or qualities being borne along steadily from cell to cell in the divisions must be thrown into a latent condition, or perhaps totally lost, while simultaneously or separately, other qualities may be acquired by what actual operation we do not know. It seems fairly obvious, however, that these saltations arising from the non-uniform action of the chromosomes, must take place in response to some stimulus outside of the protoplast in which it actually occurs. This by no means supposes that the stimulation comes from climatic, or other environmental factors, but in all probability results from enzymatic or other action from neighboring

masses of cells. If this is so then we may hope to be able to duplicate the process in our cultures and call out a proportion of mutants at our will. The results of experiments now in progress seem to lend great favor to this assumption.

This view of the case is also favored by the facts offered by bud-sports, which have been designated as "vegetative mutants, although as shown above, all mutations are essentially of a vegetative character. In the simplest forms of these sports, lateral buds arising generally near the base of a shoot develop branches which diverge definitely from the characters of the main shoot, and which usually coincide with some known form, although this is not always the case. Sometimes entirely new forms arise in this manner as in the case of seed-mutants. During the present season I have been so fortunate as to have three notable examples of bud-sports in the experimental cultures. One of these was a basal branch of *Oenothera ammophila* which sported into the characters of *O. biennis,* and suggesting a possible hybrid ancestry with the latter species as one of the parents. A second case was one in which a seed-mutant of *O. biennis* gave a bud-sport which bore the characters of the ancestral type or the true *O. biennis.* A third case was one in which a plant of one of the numerous types embraced in a complex hybrid progeny bore a branch which sported in a branch which resembled a sister type. Other anatomical relations are found. Thus a bud-sport may embrace not only a branch, but a portion of the main stem, from which it arises, or in other cases it may include a section or longitudinal strip along one side of a branch even dividing a flower or fruit, while in other cases it may be represented by single flowers or fruits scattered indiscriminately through an inflorescence.

It is to be noted that in most if not all of the sectorial variations by which a part of a bud bears the divergent



Lamarck's Evening-primrose and Ten of Its Mutants. The dense rosette in the lower left-hand corner is *O. Lamarckiana,* the parental form. *O. gigas* is in the upper right-hand corner, and under it is *O. scintillans*. The irregular rosette above *O. Lamarckiana* is *O. albida,* and to the right of *albida* is *lata*. *O. oblonga* is in the upper left-hand corner.

characters, the change is a reversionary one, and the qualities that appear are really latent in the entire plant, and only need some stimulus to awaken them, or some agency to weaken the dominancy of the prevalent characters.

In the case of the appearance of characters not hitherto borne by the main stock, the case is not so clear, especially as we feel fairly certain that the saltations do ensue, in seed-mutants at least, in single cells. Here the theoretical side of the case seemed least supported by facts and I set about supplying the deficiency with what success you may presently judge.

Bud-sports are usually found on the basal portions of main stems of shoots, or in that part of the main axis, which often shows juvenile structures, so that we may say that these breaks in heredity are very frequent in the closing part of the embryonic period, although sometimes occurring much later. On the other hand, the changes which result in the formation of seed-mutants must ensue in the very closing stages of the sporophyte, and here is encountered a feature not recognized in bud-mutations, that of a fairly constant frequency, which in itself would suggest internal causes. It was determined however to attempt to induce or influence mutation in one of these periods. It was deemed impracticable to attempt this in the early life of the sporophyte and attention was given entirely to the stage immediately preceding the reducing divisions.

Omitting the detail of technique I may say that strong osmotic reagents, and weak solutions of stimulating mineral salts were injected into ovaries in such manner that unfertilized ovules were subjected to the action of the fluids, which killed many of them, but which gave the much desired results in a few. In *Lamarckiana* and *biennis* the frequency and character of the known mutants was unaffected, but in the progeny of the latter species was found a single individual constituting a type hitherto un-

known. This single aberrant individual might have been a mutant of low frequency, comparable to *gigas* derived from *Lamarckiana,* and its recurrence here might have been merely a matter of chance. However, in another species of evening-primrose, *Raimannia odorata,* a flower which belongs to a separate genus of the family, and is not known to be mutating, the treatment described resulted in a large number of aberrant individuals of a hitherto unknown type. Some of these, which show a shorter life-cycle than the parental form, and many anatomical divergencies, have been brought to bloom and to maturity, and the new form is obviously a potential species. In this experience, exemplified by specimens of the normal, parental forms, and aberrant mutants, I am able to offer you conclusive proof that agencies external to the cell may induce mutations, and consequently exert a profound influence on heredity. It would not be well to exaggerate the importance of this result, yet it is evident that the establishment of this fact marks a long step forward in the experimental study of inheritance and the origin of species.

A brief summary of the foregoing discussion may be made in the following generalizations:

1. Species may arise by hybridizations which result in fixed forms. A large number of forms known as species and recognized to be of such origin are known and a number of them have been duplicated in experimental cultures, some of which were made over a half century ago.

2. The mutation theory groups an enormous number of hitherto unexplainable facts, to which we are constantly adding in great volume, into a connected and meaningful whole, and best of all it brings the subject anew into a condition where it is amenable to experimental methods, in the laboratory, and experimental garden.

3. As a result of the theoretical conceptions offered us,

we have been able to make repeated observations of the general principles which govern breaks, or saltations in heredity, and to observe in what manner such mutations are connected with the origin of species.

4. Having ascertained at what time in the life-period of the individual mutations occur, I have been so fortunate as to secure results, demonstrating that mutations may be induced in a species not hitherto active in this respect, and that it is possible to call out new species by the intervention of external agents during the critical period.

5. Not less important than the foregoing is the unavoidable implication that breaks, saltations, or discontinuous action may be caused in inheritance by forces external to the protoplasts, and cells which are the true bearers of the hereditary characters.

Lastly it is of the greatest interest to note that in the effort to correlate the larger generalizations in the various departments of science in the concept of mutation we have hit upon a principle strongly favored by a modern system of mathematics, well exemplified by the spontaneous breaking-up and rearrangement of the complex atoms in radium, uranium and allied metals, and which has been recognized by Prof. George Darwin, the physicist, in the following words: "These considerations lead me to express a doubt whether biologists have been correct in looking for continuous transformation of species. Judging by analogy we should rather expect to find slight continuous changes occurring during a long period of time, followed by a somewhat sudden transformation into a new species, or by rapid extinction."

In the long-continued narrowing of the range of fluctuation in the various organs, coming to saltations, or direct origination of new forms, as the plant passes from generation to generation, we have as perfect a fulfilment of this motion as might be expected when an attempt is

made to interpret the action of the living by the properties of the non-living.

DANIEL TREMBLY MACDOUGAL.

NEW YORK BOTANICAL GARDEN.

1865-